POPULATION DENSITY AND DISPERSAL ABILITY IN DARWIN'S DARKLINGS: FLIGHTLESS BEETLES OF THE GALÁPAGOS ISLANDS[1]

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Abstract.—This study is the first to combine both field and genetic data to examine population structure in flightless beetles from the Galápagos Islands. Field studies were conducted on four species of tenebrionid beetles belonging to three genera, *Ammophorus* Gúerin-Méneville, *Blapstinus* Latreille, and *Stomion* Waterhouse. The dynamics of the beetle community at the study site, Tortuga Bay, Santa Cruz Island, were analyzed in an attempt to examine patterns of activity and to quantify species abundances, population sizes, densities and levels of individual vagility. Beetle activity was found to vary with temperature, precipitation and number of sunlight hours. Although the number of recaptures was low, densities in the quadrats ranged from eight *B. lugubris* Boheman per hectare to 1238 *S. laevigatum* Waterhouse per hectare. Individual vagility is shown to be low among *S. laevigatum*, the most abundant species at the study site, as the dispersion index (DI) showed that captures were aggregated in three of the four quadrats, suggesting little movement. In addition, beetle captures occurred more frequently than expected in internal traps, again revealing limited movement into or out of the quadrats. These results were confirmed by a separate analysis of genetic differentiation among demes of *S. laevigatum* which showed the number of migrants to be less than one per generation.

Key Words.—Insecta, Coleoptera, ecology, mark and recapture, population structure, tenebrionid beetles

The Galápagos Islands have provided striking examples of species radiations under conditions of allopatry. The role of geographic isolation in island archipelagoes has long been recognized in limiting gene flow and promoting reproductive isolation (Mayr 1963). Geographic isolation may also be imposed by life-history parameters such as low dispersal ability or flightlessness. Isolation may also result from habitat restriction, whereby populations are spatially separated by regions of unsuitable habitat (King 1987, Crouau-Roy 1989), or by host plant specificity (McCauley & Eanes 1987). Genetic studies on flightless insects (Zera 1981, Finston & Peck 1995) and birds (Baker et al. 1995) have revealed high levels of genetic differentiation among populations and low genetic variability.

The migration of individuals can be measured using both direct and indirect methods. Mark and recapture studies can be used to directly measure individual vagility and provide estimates of the number of migrants between demes. In particular, pitfall traps have commonly been used in population studies of surface dwelling insects, although their use is highly dependent upon a number of factors, including vagility of the organism under study, and ecological factors such as the influence of substrate type, vegetation and weather patterns on activity levels (Ahearn 1971, Thomas & Sleeper 1977). Alternately, population genetic structure

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can be measured, and the amount of gene flow and migration inferred. Investigations into the role of limited vagility may provide an insight into patterns of microevolutionary change. The extent of isolation and gene flow among spatially separated populations determines the potential for phenotypic and genetic differentiation. Indeed, speciation is most active where geographic barriers are greatest-among insular habitats (Mayr 1942, 1966).

Prior work on species radiations in the Galápagos Islands has focused on the vertebrate fauna (Van Denbergh 1914, Hendrickson 1966, Lack 1968, Grant 1986), however, the invertebrate fauna also provides striking examples of species radiations (Coppois 1984, Peck & Kukalova-Peck 1990). In particular, the Galápagos supports a rich assemblage of tenebrionid (darkling) beetles. Darkling beetles are often abundant members of surface dwelling communities in arid and semi-arid environments (Crawford 1990). Tenebrionid species occur sympatrically in arid regions all over the world (Thomas 1983), and most are flightless, night active members of these communities (Doyen & Tschinkel 1974). A total of 51 species are known in 14 genera from the Galápagos Islands. Most notable are Darwin's darklings, *Ammophorus* Gúerin-Méneville, *Blapstinus* Latreille, and *Stomion* Waterhouse, three genera containing 38 described species of flightless, ground-dwelling beetles (Peck & Kukalova-Peck 1990). Collectively, this group represents the largest radiation of beetle species in the archipelago. Four of these species, belonging to all three genera, were found sympatrically at a single site, and were the focus of this study. The present study represents the first attempt to quantify population sizes, densities, species abundances and beetle activity in a tenebrionid community in the Galápagos Islands, and provides the first examination of dispersal ability in a Galápagos insect, employing both field and population genetic data.

MATERIALS AND METHODS

The present study involved two field components: a mark and recapture study, and a weekly transect study. The field site was the dune area located at Tortuga Bay on the island of Santa Cruz, Galápagos. Beetles were identified using the key of Van Dyke (1953). Field work took place March to July, 1992.

Mark and Recapture Study.—In order to assess species assemblages, population sizes and densities, and dispersal ability, four separate quadrats were arranged, each consisting of five rows of five traps. Each trap was 2 m from any other trap in a quadrat, and consisted of small, unbaited cylindrical plastic containers 10 cm in diameter and 6 cm deep. Each trap was equipped with a cover which was used to close the traps and a coarse wire screen (used when the traps were open) to prevent beetle predation by birds and lizards. Each quadrat covered 64 m². The quadrats were arranged as in Fig. 1, such that each quadrat was situated in the corner of a 32 m × 102 m rectangle.

The vegetation was not homogeneous over the entire study area; the quadrats differed both in plant species present and in the proportion of ground covered by vegetation. The plant composition in order of abundance for each quadrat is as follows, with the estimated percent of ground cover noted in brackets: I. *Scaevola plumieri, Ipomoea pes-caprae, Sesuvium portulacastrum, Heliotropium sp.*, some grasses (80%); II. *Scaevola plumieri, Ipomoea pes-caprae, Sesuvium portulacastrum, Prosopis juliflora* (90%); III. *Scaevola plumieri, Sesuvium portulacastrum,*
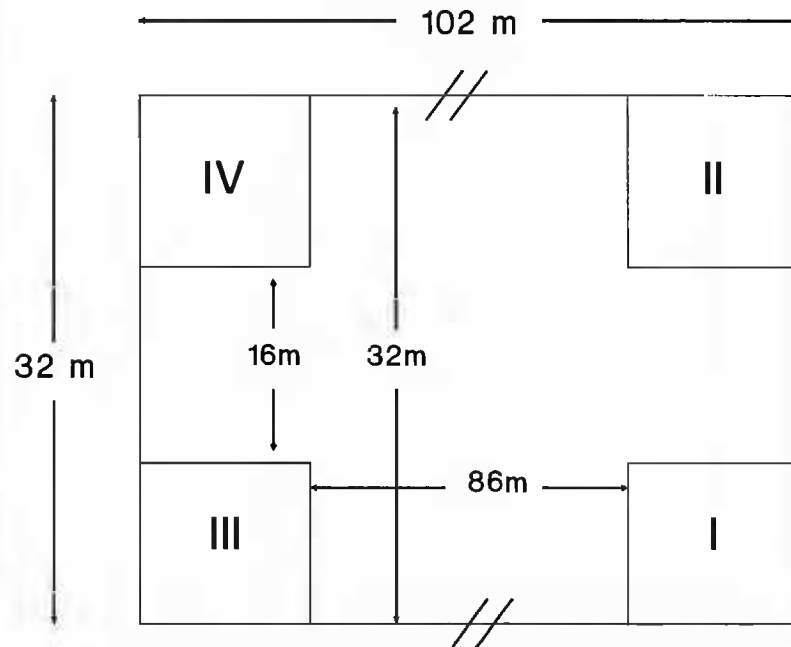
Figure 1.   Arrangement of traps and quadrats used in the mark and recapture study.

Ipomoea pes-caprae, Heliotropium sp. (60%); IV. *Heliotropium sp., Tiquilia darwinii, Cryptocarpus pyriformis, Prosopis juliflora* (15%).

The traps were opened for a twelve hour period, from dusk to dawn, at five day intervals from 15 Jun to 8 Jul 1992. Individuals caught in the traps were recorded by quadrat and trap number, and marked with a dot of white typing correction fluid in the corner of the elytron which corresponded to the quadrat in which it was caught. Thus, recaptured individuals could be identified with respect to their original quadrat of capture. The beetle was then released at the site of capture. Estimates of population size (N) were calculated for those quadrats in which marked beetles were recaptured using the geometric model described by Thomas & Sleeper (1977):

$$N = M/[1 - (M/t)]; \ s^2 = M^2 t(t - r)/r^3$$

where M = number of individuals marked; r = number of individuals recaptured, and t = total number of captures (= total number marked + recaptures). This model was chosen because it does not assume equal catchability rates among individuals, and minimizes stochastic events by permitting the use of cumulative results. Population density was calculated by dividing N by the unit area in hectares.

The dispersion index (DI) was calculated for *S. laevigatum* Waterhouse only, the most abundant beetle in the quadrat area. The DI (variance/mean) approximates unity when individuals are randomly distributed; a higher DI suggests aggregations of individuals (Fowler & Cohen 1990). A chi-square analysis was used to test the random distribution of individuals in each of the four quadrats. In addition, a chi-square test of the observed and expected number of captures (assuming a uniform distribution) from peripheral and internal traps was performed as a further inspection of the dispersal habits of *S. laevigatum*.

Transect Census.—As an independent assessment of community assemblages and beetle activity, a 100 m transect was marked along a one m wide foot trail which crossed the littoral and arid vegetation zones. The substrate changed from a fine white marine sand to volcanic rock approximately 20 m from the start of the transect. Sampling took place every five days and continued for eight weeks,

from 8 May to 7 Jul 1992. Baits of 5 gm of dry oatmeal were laid out at 2 m intervals at dusk, such that each bait site covered approximately 2 m ^{2}. The transect was inspected one hour later, beginning at the site closest to the beach. The numbers of individuals of each species belonging to the three tenebrionid genera were recorded for each bait site. In order to examine the effects of local climatic conditions on species abundance and activity, weather data collected at the Charles Darwin Research Station was used for analysis. The research station lies approximately 2 km from the study site at Tortuga Bay, and is thus representative of the climatic conditions at the study site. Data included in this analysis were temperature and humidity at 18:00 h, total precipitation, number of hours of sunlight, and minimum and maximum temperatures for the day in which the count was made. In addition, the total precipitation for the seven day period preceding each sampling date was used. Pearson correlations and their corresponding probabilities were calculated between these ecological data, and weekly species richness (number of different species found in the evening's collection) and individual species abundances using the CORR module in SYSTAT (Wilkinson 1988).

Genetic Analysis.—*Stomion laevigatum* were collected from the following 5 sites on 4 different islands: Caamaño-sea lion beach (CAAM); Isabela-Alcedo Rim (ARIM), Tagus Cove (TAGU); Santa Cruz-Tortuga Bay (BTOR) Santiago-Playa Espumilla (SANT). Where possible, 44 individuals were analyzed for variation at eight polymorphic enzyme loci using cellulose acetate electrophoresis (Hebert & Beaton 1993). The loci analyzed were as follows: hexokinase (*Hk-2*), mannose-6-phosphate isomerase (*Mpi*), phosphoglucomutase (*Pgm-1*), peptidase-A (*Pep*, utilizing phe-pro), supernatant and mitochondrial glutamate oxaloacetate transamerase (*Got-s*, *Got-m*), 6-phosphogluconate dehydrogenase (*6pgdh*), and phosphoglucose isomerase (*Pgi*). Genetic analyses were carried out using BIOSYS-1 (Swofford & Selander 1991) unless otherwise indicated. Allele frequencies were calculated for each site, and Wright's F-statistics were analyzed hierarchically such that gene frequency divergence could be measured among demes on the same island as well as among demes on different islands. (Wright 1940). Two models of gene flow were employed to obtain estimates of the number of migrants between demes. Wright's F-statistics were used to calculate the number of migrants using the following formula:

$$F_{ST} = 1/(4N_m + 1)$$

where N_m = the effective number of migrants per generation. Slatkin's rare alleles model (Slatkin 1985, 1987) was used to directly estimate the number of migrants between demes using the frequency of unique alleles as indicators of gene flow:

$$\ln [p(1)] = a\ln(N_m) + b,$$

where $p(1)$ is the average frequency of alleles found only in single populations and a and b are constants that depend on the population size. In order to use Slatkin's constants which were based on a sample size of 25, N_m was multiplied by the ratio 25/n where n is the mean sample size of those populations possessing unique alleles (Slatkin 1985, 1987).

RESULTS

Mark and Recapture Study.—Four species, *Ammophorus bifoveatus* Waterhouse, *Blapstinus lugubris* Boheman, *B . spatulatus* Van Dyke, and *Stomion lae-*

Table 1. The total number of individuals marked/recaptured for each species for all four quadrats.

Week	A. bifoveatus	B. lugubris	B. spatulatus	S. laevigatum
1	7/0	0/0	22/0	36/0
2	20/0	0/0	30/1	42/0
3	5/0	0/0	28/1	44/0
4	2/0	0/0	19/1	25/0
5	3/1	1/0	10/0	24/0
Total	37/1	1/0	119/3	171/0

vigatum were found at the study site. Of the 328 beetles captured, marked, and released, only four were recaptured (Table 1). A single individual of *A. bifoveatus*, three individuals of *B. spatulatus*, and no individuals of *S. laevigatum* or *B. lugubris* were recaptured. All four individuals were recaptured in their original quadrat of capture. Population sizes obtained from the model presented by Thomas & Sleeper (1977) are not reported here, as the estimates resulted in standard deviations which approached or exceeded the estimates themselves. Because of the poor recapture rate, population density was instead calculated each week by dividing the total number of individuals of each species in a quadrat by the unit area (64 m²). The arithmetic mean over all four quadrats was then calculated over all weeks. Density estimates ranged from 8 *B. lugubris* per hectare to 1340 *S. laevigatum* per hectare (Table 2).

The DI showed that *S. laevigatum* captures were not random in three of the four quadrats, as this ratio approximated unity only in quadrat I (Table 3). Some traps caught large numbers of beetles, while others caught no beetles over the course of the study. Tests of distribution models showed that aggregation of beetles occurred in quadrats II, III and IV. Quadrat I fitted neither a Poisson nor a binomial distribution, although its chi-square value (8.00) was very close to the critical value (7.81) for acceptance of the random (Poisson) distribution model. Furthermore, a chi-square test showed significant deviations between the number of observed and expected captures in both peripheral and internal traps. Beetle catches occurred more frequently than expected in the internal traps and less frequently in the peripheral traps in three of the four quadrats (Table 4).

The number of captures per quadrat was not found to be significantly related to the estimated amount of vegetation cover (Pearson correlation = 0.765, P = 0.235), but the greatest number of captures did come from quadrats I and II,

Table 2. Weekly density estimates (per hectare) for four tenebrionid species averaged over each of four quadrats.

Week	S. laevigatum	B. lugubris	B. spatulatus	A. bifoveatus
1	1410	0	860	270
2	1640	0	1170	780
3	1220	0	1090	190
4	980	0	740	80
5	940	40	390	120
Mean	1340	8	850	288
(±SD)	(294.5)	(17.9)	(309.8)	(284.4)

Table 3. Mean number of catches per trap ($\bar{x}$), standard deviation (SD), dispersion index (DI) and chi-square values (χ^2) for random (Poisson) and aggregated (binomial) distribution model tests for each of four quadrats in the mark and recapture study. * = $P < 0.05$.

Quadrat	$\bar{x}$	SD	DI	Poisson χ^2 (df)	Binomial χ^2 (df)
I	1.80	1.83	1.02	8.00* (3)	8.93* (2)
II	3.44	5.24	1.52	25.98* (9)	8.72 (8)
III	0.60	0.92	1.53	6.32* (2)	2.04 (1)
IV	1.12	1.69	1.51	14.10* (4)	7.67 (3)

which were estimated to be 80% and 90% vegetated, respectively. The fewest captures came from quadrats III and IV, which were an estimated 60% and 15% vegetated, respectively. *Stomion laevigatum* was the most abundant species in all four quadrats. *Ammophorus bifoveatus* and *B. spatulatus* were particularly rare in the less vegetated quadrats. No *A. bifoveatus* were captured in quadrat III and *S. laevigatum* was more than four times more abundant than *B. spatulatus*. In quadrat IV, *S. laevigatum* was twenty-seven times more abundant than *B. spatulatus* and fourteen times more abundant than *A. bifoveatus*. *Blapstinus lugubris* was captured only once, in quadrat II.

Transect Census.—The four species found in the quadrat area, *A. bifoveatus*, *B. lugubris*, *B. spatulatus*, and *S. laevigatum* were also found along the transect. A total of 1199 beetles were encountered, with *B. spatulatus* and *A. bifoveatus* being most common (Table 5). In contrast to the mark and recapture site, *S. laevigatum* was the least abundant species encountered. Evening beetle counts ranged from two to 208 individuals, and the number of species observed ranged from one to four.

Correlation of species abundance and richness with seven environmental conditions showed significant but negative correlations for several variables (Table 6). For example, the number of individuals of *B. spatulatus* and *A. bifoveatus* were negatively correlated with maximum daily temperature, temperature at 18:00 h, the days' precipitation, hours of sunlight during the day, and the total precipitation for the week preceding the sampling date. In contrast, the number of different species observed in a sample was shown to be positively correlated with percent relative humidity. The days' minimum temperature showed no effect on species abundance or diversity. The numbers of *S. laevigatum* and *B. lugubris* were not correlated with any measured environmental conditions.

Table 4. Chi-square test of number of expected versus number of observed captures in internal and peripheral traps for four quadrats. * = $P < 0.05$. df = 1.

Quadrat	Internal Obs.	Internal Exp.	Internal χ^2	Peripheral Obs.	Peripheral Exp.	Peripheral χ^2
I	13	16.2	0.632	32	28.8	0.356
II	43	31.2	5.38	41	53.8	3.03
III	7	5.4	0.474	8	9.6	0.267
IV	12	10.1	0.366	16	17.9	0.206
Total			6.852*			3.859*

Table 5. The number of individuals of each of four species of tenebrionids counted at the Tortuga Bay transect site on Santa Cruz Island, Galápagos.

Week	S. laevigatum	B. lugubris	B. spatulatus	A. bifoveatus
1	2	0	0	0
2	9	4	37	37
3	4	44	58	96
4	1	0	53	74
5	5	19	65	73
6	1	14	80	112
7	1	8	89	110
8	2	19	69	113
Totals	25	108	451	615

Genetic Analysis.—Although there were no allelic substitutions among sites at any of the eight loci surveyed for *S. laevigatum*, allele frequencies did differ among sites (Table 7). Genetic differentiation was substantial among demes at both hierarchical levels, where on average, nearly 40% of the total observed variation in allele frequencies was due to variation among demes, whether on the same island or on different islands (Table 8). Approximately 60% of the variation resulted from differences within demes ($1-F_{ST}$). Both models of gene flow produced migration estimates of considerably less than one migrant per generation among demes (Table 8). Wright's model produced an estimate of 0.429 migrants per generation among demes on the same island and 0.383 migrants per generation among demes on different islands. Similarly, Slatkin's model produced an estimate of 0.417 migrants per generation among demes on different islands.

DISCUSSION

The utility of pit-fall traps in mark and recapture studies for the estimation of population sizes has fallen under scrutiny (e.g. Southwood 1966, Thomas & Sleeper 1977). Many non-random effects such as changes in activity patterns or abundance of populations, and biases introduced by the trapping methodology, may affect catchability and population size estimates. However, these effects can be overcome when the proper precautionary measures are observed, such as main-

Table 6. Pearson correlation coefficients for individual species' abundances and species richness and seven environmental variables. T = temperature at 18:00, PP = daily precipitation, H = relative humidity at 18:00, SOL = number of sunlight hours, TMAX = maximum daily temperature, TMIN = minimum daily temperature, TPP = total precipitation in the week preceding the collection, TI = total number of individuals in the collection, TS = total number of species in the collection. * = $P < 0.05$.

Factor	T	PP	H	SOL	TMAX	TMIN	TPP
Taxon							
S. laevigatum	0.38	−0.16	0.39	0.38	0.48	0.25	−0.07
B. lugubris	−0.23	−0.38	0.07	−0.35	−0.35	0.11	−0.36
B. spatulatus	−0.93*	−0.82*	0.52	−0.73*	−0.96*	−0.68	−0.86*
A. bifoveatus	−0.87*	−0.77*	0.37	−0.76*	−0.96*	−0.52	−0.81*
TI	−0.85*	−0.80*	0.42	−0.74*	−0.94*	−0.51	−0.84*
TS	−0.70	−0.94*	0.71*	−0.51	−0.70	−0.46	−0.93*

Table 7.   Allele frequencies for five populations of *S. laevigatum*. *n* = sample size.

Pop. *n*	SANT 44	BTOR 44	CAAM 42	TAGU 43	ARIM 44
HK-2					
3	0.989	0.977	1.000	1.000	1.000
4	0.011	—	—	—	—
5	—	0.023	—	—	—
MPI					
2	0.034	—	—	0.012	—
3	0.375	—	0.012	—	0.080
4	0.580	0.372	0.666	0.928	0.920
5	0.011	0.581	0.012	0.060	—
6	—	0.047	0.310	—	—
PGM-1					
1	0.011	0.011	—	—	—
2	0.011	0.034	—	0.058	—
3	0.967	0.921	0.857	0.907	0.989
4	0.011	0.034	0.143	0.035	0.011
PEP					
2	—	0.284	0.119	0.081	0.080
3	0.989	0.693	0.881	0.919	0.920
4	0.011	—	—	—	—
5	—	0.023	—	—	—
GOT-M					
2	0.625	—	0.488	0.907	0.909
3	0.375	0.405	0.512	0.093	0.091
4	—	0.595	—	—	—
GOT-S					
1	0.012	—	—	—	—
2	0.035	—	—	—	—
3	0.720	0.667	—	—	—
4	0.233	0.333	0.561	—	0.966
5	—	—	0.439	1.000	0.034
6PGDH					
2	—	0.035	0.012	0.012	—
3	1.000	0.930	0.988	0.163	0.068
4	—	0.035	—	0.826	0.898
5	—	—	—	—	0.034
PGI					
1	—	0.023	—	—	—
2	0.125	0.080	—	0.186	0.011
3	0.546	0.874	1.000	0.791	0.989
4	0.295	0.023	—	—	—
5	0.034	—	—	0.023	—

taining uniform trap size and distance between traps, as well as using unbaited traps (Thomas & Sleeper 1977). Moreover, some surface-dwelling arthropods, such as tenebrionids, may be particularly amenable to pit-fall trapping techniques. This method was shown to be most effective in evaluating changes in population

Table 8. Estimates of the number of migrants per generation using two models of gene flow. F_{ST} = Wright's F-statistic, N_m = number of migrants.

Subgroup (S)	Total group (T)	F_{ST}	N_m (Wright)	N_m (Slatkin)
Site	island	0.368	0.429	—
Site	total	0.395	0.383	0.417

behaviour, density, and dispersal, but least effective at obtaining estimates of population size (Ahearn 1971). The number of recaptures in the present study was too few to allow a reliable estimation of population size for any of the species, therefore, distribution, population density and vagility of the beetles were all examined in the quadrats using the total number of captures.

Capture success may have been a function of both trapping methodology and patterns of beetles activity and abundance. For example, mortality rates may have been higher in marked beetles, that is, the correction fluid may have been toxic (although no dead, marked beetles were found in the study area), or they may have been more visible to predators. Alternately, the mark may have rubbed off during the course of the study as the beetle brushed against vegetation or sand while scavenging, although marked beetles held in captivity during the course of the study did not lose their markings (pers. obs.). Individual ranges may have been larger than the area covered by the four quadrats. Beetles, once marked, may have wandered out of the area. Finally, weekly patterns of beetle activity may also have been a contributing factor. Beetle activity on any given day may be affected by temperature, relative humidity, moon phase, recent rainfall, or amount of cloud cover (Thomas 1979). Indeed, the results of the transect study suggested that for at least two species, sand temperature and humidity may affect beetle activity and therefore recapture success. The highest number of evening sightings occurred following days with the lowest number of sunlight hours (less than five hours), perhaps as a result of lowered sand surface temperatures. In addition, the greatest species richness was noted on evenings with the greatest degree of daytime relative humidity, suggesting that cooler temperatures and some moisture favoured beetle activity. However, beetle activity was greatly reduced during heavy rains, such as on the first evening of collection.

Density estimates made from the total capture data were generally lower but in accordance with estimates for tenebrionids from other mark and recapture studies, ranging from 8–1340 beetles/hectare. Ahearn (1971) found the average density for five tenebrionid species to be about 1700 beetles/hectare at a site in South Mountain Desert Park in Phoenix, Arizona. Thomas & Sleeper (1977) found a range of 96–2755 beetles/hectare for six species in Rock Valley, Nevada. Similarly, Thomas (1979) found approximately 1000 beetles/hectare for the two most abundant species over a two year period in the Mojave Desert.

The results of this study further suggested that Darwin's darklings may have limited vagility. If individuals had large ranges, or good dispersal tendency, we would expect to capture some beetles in a quadrat different from that in which they were marked, or outside the quadrats. However, of the four beetles which were recaptured, each was found in the same quadrat in which it was marked. In addition, active searches in the area surrounding the quadrats produced no marked

beetles. Because each beetle was recaptured in its original quadrat of capture, no direct estimates of displacement distances could be made. However, the DI for *S. laevigatum* showed that beetles tended to be aggregated in three of the four quadrats, suggesting little movement, although the use of pheromones as attracting agents cannot be discounted in explaining the observed aggregations. In addition, an analysis of the number of beetles trapped in peripheral and internal traps showed that more beetles were trapped in the internal traps than the peripheral traps. If populations were vagile, we would expect to trap more beetles in the peripheral traps, as beetles move in from the surrounding area. Doyen & Tschinkel (1974) found vagility to be low among some tenebrionid species in their study in the Chiricahua Mountains; beetles were frequently recaptured in the same or a nearby quadrat as that in which they were marked, and taxa which showed the greatest levels of aggregation were those which were least vagile. The comparatively low number of *S. laevigatum* at the near-by transect site also suggests that this taxon is limited in its range. These results were confirmed by an analysis of genetic differentiation among demes. Estimates of the number of migrants among demes using both Wright's F-statistics and Slatkin's rare alleles model for *S. laevigatum* showed dispersal to be very low, revealing less than one migrant per generation for both models (Finston & Peck 1995).

The dispersal ability of individuals of a species is largely responsible for the establishment and maintenance of geographical isolates (Mayr 1966:565). Darwin's darklings show narrow distributions; each species is found on only one or a few geographically close islands (Van Dyke 1953). The flightless condition of the beetles limits their dispersal ability, particularly across water gaps. Peck (1994a,b) showed that various Coleoptera are occasionally present as aerial plankton or as pleuston between islands in the archipelago. Darwin's darklings, however, range from 5–10 mm and are larger than the small-bodied Coleoptera typically found as aerial plankton. It is likely that only single or few founding individuals, carried as sea surface pleuston, were responsible for the colonization of new islands. Although the Galápagos climate is semi-arid, it is seasonal, having both a wet and a dry season. Nevertheless, as with other, more stable tropical habitats, there may be little pressure for seasonal movement of beetles in search of favourable habitats. Furthermore, the highly stratified vegetation zones of the islands (Wiggins & Porter 1971) may pose geographical barriers for tenebrionid beetles, which are largely restricted to the littoral and arid zones (Van Dyke 1953, Finston 1993). This, and a previous study (Finston & Peck 1995) showed that dispersal ability and gene flow are limited even on a local scale; the number of migrants between populations was less than one per generation between populations on the same island. The potential for few founders and limited subsequent movement of flightless beetles provides a model for the establishment and maintenance of geographical isolation of populations. Such isolation is necessary for microevolutionary change- localized differentiation through both adaptation and stochastic events such as founder effects and genetic drift- and ultimately, speciation.

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